PAPERS.

13. On the Organ of Jacobson and its Relations in the "Insectivora."—Part I. *Tupaia* and *Gymnura*. By R. Broom, D.Sc., M.D., C.M.Z.S.

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(Plates I. & II.*)

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In 1897, in "A Contribution to the Comparative Anatomy of the Mammalian Organ of Jacobson," published in the Trans. Roy. Soc. Edin., I called attention to the very great value of a study of the morphology of the cartilages connected with Jacobson's organ as a guide to the affinities of aberrant mammals. Changes in habit bring about most marked alterations in teeth, bones, and many viscera, but the delicate little cartilages in the nose are so little affected that we find almost exactly the same type of structure in forms so dissimilar as the sheep, cat, hedgehog, bat, and lemur. And as the arrangement is an extremely complicated one, we seem justified in concluding that the similarity indicates affinity and common origin of those types rather than independent developments of this remarkable structure.

So far as at present known there are only two main types of the organ of Jacobson and its relations found in mammals: (1) the primitive or Marsupial type, which is a simplification of the type found in the Monotremes, and which is retained with slight modifications in such forms as *Dasypus*, *Orycteropus*, and the Rodents; and (2) the higher Eutherian type found in Ungulates, Carnivores, *Erinaceus*, the bat *Miniopterus*, *Lemur*, and *Procavia*.

In 1902 I examined the organ in *Macroscelides*, hoping, in view of Parker's discovery of marsupial characters in the skulls of the allied *Petrodromus* and *Rhynchocyon*, that I might find some type intermediate between that of the Marsupial and that of *Erinaceus*. To my great surprise I found that in its relations the organ in *Macroscelides* has no resemblance whatever to that of the typical Insectivore, but agrees in practically every detail with the type seen in the marsupial *Perameles*.

In my paper "On the Organ of Jacobson in the Elephant Shrew (*Macroscelides proboscideus*)" which appeared in the Proc. Zool. Soc. 1902, vol. i. p. 224, I came to the conclusion that, "from the fact that *Macroscelides* agrees with the Marsupials in every detail of the anatomy of this region, we are forced to the conclusion that it is a very near relative of the Marsupials,

* For explanation of the Plates see p. 162.

and has probably very little affinity with the more typical Insectivores."

When my paper was written I was in the Karroo, far from any libraries, and I was not aware that in 1864 Peters had divided the Insectivora into two groups: (A) those with an intestine with a large cæcum, including "Galeopitheci," "Tupayæ," and "Macroscelides"; and (B) those with intestine simple, without cæcum, including "Centetinæ," "Erinacei," "Talpina," and "Sorices."

Haeckel in 1866 definitely divided the Insectivora into two suborders: (1) Menotyphla, including the families Cladobatida, with *Cladobates* and *Tupaja*, and Macroscelidia, with *Macroscelides* and *Rhynchocyon*; and (2) Lipotyphla, including the families Soricida, Talpida, Erinaceidea, and Centetida.

Though most later workers have regarded the Insectivora as a single natural group, Leche (1884) has suggested separating the Menotyphla as a distinct order, and Gregory, in his recently published work on 'The Orders of Mammals' (1910), places the typical Insectivora in the Superorder Therictoidea, and the Menotyphla as an order of the Superorder Archonta, together with Dermoptera, Chiroptera, and Primates.

For some time I have been most anxious to examine the organ in *Tupaia* to see how far it agreed with *Macroscelides*, and fortunately I was able to obtain from the American Museum a very good specimen, preserved in formalin, of a young *Tupaia*, and for comparison a young specimen of *Gymnura*. Both specimens had been obtained in Borneo by Mr. C. W. Beebe. Prof. J. P. Hill's laboratory assistant, Mr. F. Pittock, has kindly sectioned for me by microtome the *Gymnura* snout, but owing to the extreme hardening of the *Tupaia* specimen the snout had to be cut by hand. Both specimens show all the desired characters satisfactorily.

The Organ of Jacobson in Tupaia.
(Plate I.)

The nose in *Tupaia*, unlike that of *Macroscelides*, does not extend very much in front of the premaxillary bone, and the nostrils are nearly terminal, but look more outwards than forwards.

A section passing through the nostril shows the nasal cartilages forming a median septum with a well-developed alinasal cartilage above and a small cartilaginous extension forming the nasal floor. A few sections further back, the anterior part of the inferior turbinal is seen in section, attached to the upper part of the nasal wall, and showing the opening of the naso-lacrimal duct on its side. Immediately behind the nostril the inferior turbinal is seen rising vertically from the nasal floor. The nasal-floor cartilage is still attached to the base of the septum but is small, and there is no cartilage in the external wall of the nasal passage.

Pl. I. fig. 1 shows a transverse section passing through the front of the premaxillary bone. Here the nasal-floor cartilage is seen detached from the septum, and forms not only the floor but the support for the inferior turbinal. The anterior part of the outer cartilaginous wall is also seen cut across.

Fig. 2 cuts through the first incisor and the anterior part of the papilla of the palate. The nasal-floor cartilage is seen connected with the cartilage of the lateral wall and forming the cartilaginous support of the inferior turbinal. The great size of the papilla is well seen. The appearance of the structures in this section resembles considerably a similar section through the snout of *Didelphys*, and also somewhat a similar section through the snout of *Dasypus*.

Fig. 3 represents a section nearly 1 mm. behind that represented in fig. 2. The papilla is seen occupied by a large papillary cartilage. The recurrent nasal-floor cartilage has the inner portion enlarged where it is about to become Jacobson's cartilage. The inferior turbinal is further up on the lateral nasal wall. This section resembles a corresponding section through the snouts of any of the Polyprotodont marsupials. In the structure of the nasal cartilages the resemblance is rather with *Dasyurus* and *Didelphys*; in the great development of the papilla and its cartilage the resemblance is more with *Perameles*.

Figs. 4–6 represent three sections close to each other, and only a short distance behind that shown in fig. 3. They illustrate the relations of the naso-palatine canal, and the opening of the organ of Jacobson into the nasal cavity. The peculiar structure which I have elsewhere called the outer bar of Jacobson's cartilage is well seen. In fig. 4 it is attached to the upper part of Jacobson's cartilage. In fig. 5 it is free, and in fig. 6 attached to the lower portion of Jacobson's cartilage. The structures in these sections are typically Polyprotodont marsupial and resemble those of *Perameles* as much as those of *Perameles* do those of *Dasyurus* or *Didelphys*, and considerably more than do those of any known Diprotodont marsupial.

The outer bar of Jacobson's cartilage is believed to represent the remains of the turbinal of Jacobson's organ in the Monotremata. It is present in all marsupials, in *Dasypus*, *Orycteropus*, *Macroscelides*, and some Rodents, but is unknown in any of the higher mammals.

Fig. 7 represents a section considerably further back than that shown in fig. 6. Here Jacobson's organ is seen well developed, with a single blood-vessel on its outer side and another on its inner, exactly as in *Perameles* and *Didelphys*. Jacobson's cartilage has the usual shape, and is supported internally and below by the palatine process of the premaxillary. Along the floor of the nasal cavity is a distinct posterior nasal-floor cartilage. This is the only structure in the snout that is not typically Polyprotodont marsupial. As the structure is well developed in *Echidna*, it is manifest that in this respect *Tupaia*, which retains

it, is more primitive than the Polyprotodont marsupials which have lost it. It is very well developed in the Rodent, *Lepus*. In *Macroscelides* it is only slightly developed in the young specimens which I examined, but may be better developed in the adult.

Fig. 8 shows a section near the posterior end of the organ. The organ is still seen to be of large size, lying in the U-shaped cartilage which it nearly fills. Jacobson's cartilage rests on the palatine plate of the maxillary, and is supported internally and superiorly by the vomer.

If the figures here given of sections of the snout of *Tupaia* be compared with those I have given of sections of *Macroscelides*, it will be seen that the two are formed on exactly the same type, and that the differences are not greater than are seen in the different families of the Diprotodont marsupials or of the Artiodactyles. Both genera agree closely with the Polyprotodont marsupials, and, as will be seen from the study of the snout of *Gymnura*, differ in almost every feature from that typical Insectivore.

The Organ of Jacobson in Gymnura.
(Plate II.)

The specimen which I have examined is a very young animal, probably recently born and about one fourth adult size. From the snout to the base of the tail measures 90 mm. Except for a few small vibrissæ on the snout it is entirely hairless.

The nostrils are nearly terminal, but open laterally, and are completely protected in front by the front of the nasal cartilage.

A section through the middle of the nostril shows a narrow septum, with above a well-developed alinasal and below a large anterior nasal-floor cartilage. The anterior end of the inferior turbinal is cut across supported by a cartilage which is connected with the outer edge of the alinasal.

A section through the posterior border of the nostril shows the anterior nasal-floor cartilage as an outer part forming the floor of the nostril and an inner narrow piece attached to the base of the septum. The turbinal is large and has a large cartilage attached to the alinasal. The lacrimal duct is seen opening on the inner side of the turbinal.

A section a short distance behind the nostril is remarkable for the rather abrupt thickening of the nasal septum and the great reduction of the inferior turbinal. The anterior nasal-floor cartilage is still attached to the base of the septum. The alinasal cartilage does not pass down on the outer wall of the nasal passage, and the cartilage, which in more anterior sections protected this wall, is reduced to a small trough of cartilage along the furrow between the small turbinal and the other nasal wall.

A few sections further back a most remarkable condition presents itself, as is shown in Pl. II. fig. 9. The broad nasal septum splits up into a median part and two lateral splints.

These lateral recurrent cartilages are structurally continuous with the base of the nasal septum and with the anterior nasal-floor cartilages. The other parts of the section are as in that previously described, except that the alinasal is curving down to form the outer nasal wall.

On passing backwards the nasal septum is found to become completely detached from the anterior nasal-floor cartilages and from the recurrent flaps which remain united to form a pair of large recurrent cartilages. This condition is seen in fig. 10. The alinasal curves round to form a complete outer nasal wall.

Fig. 11, though representing a section only a very short distance behind that of fig. 10, shows the pair of large recurrent cartilages reduced to two pairs of very small structures. As will be seen in the later sections, the upper cartilage is continued backwards to form the upper part of Jacobson's cartilage. The lower cartilage, which lies in the nasal floor, ends abruptly. The section passes through the anterior part of the premaxillary.

Fig. 12, a short distance behind the section represented in fig. 11, shows a section through the anterior part of the papilla. The upper part of the section is fairly similar to that of the previous section figured, but below the premaxillary is seen the mode of opening of the naso-palatine ducts by the sides of the small papilla. Each duct is supported by a scroll of cartilage completely round it except at the opening, and a few sections further forward show that the cartilage also protects the duct in front.

On passing backwards the cartilaginous scroll becomes divided into an upper and inner, and a lower and outer part. The former becomes the lower part of Jacobson's cartilage; the latter the posterior nasal-floor cartilage. In the section represented by fig. 13 the anterior end of Jacobson's organ is seen opening into the naso-palatine duct.

Fig. 14 represents a section a short distance further back. The palatine process of the premaxilla is seen detached. Above it lies the upper part of Jacobson's cartilage. The lower part of Jacobson's cartilage has the typical U-shaped appearance on section. There is still seen a small posterior nasal-floor cartilage.

Fig. 15 represents a section behind the anterior palatine foramen. The palatine processes of the premaxillæ give support to the cartilages of Jacobson. The organ is here well developed, and the cartilage has the form seen in most higher mammals. The nasal-floor cartilage is no longer present, the floor being supported by the secondary palatal plates of the maxillary.

Fig. 16 represents a section far behind that represented by figure 15 and near the posterior end of the organ. The organ is still fairly large and the cartilage still of the typical shape. The palatine processes do not extend so far back, and the cartilages are now in part supported by the vomer and in part by the maxillaries.

If the sections of the snout in *Gymnura* be compared with

those in *Tupaia*, it will be seen that the two differ so greatly in type that it is a little difficult to homologise some of the structures. While *Tupaia* agrees closely with the Marsupial type, *Gymnura* agrees equally well with the type found in most Eutherians. In my paper of 1897 I suggested the division of the Eutherians into two superorders—the Cœnorhinata to include those orders with the higher type of nose structure, and the Archæorhinata for those with the primitive type.

In the Cœnorhinata I placed the Carnivora, Insectivora, Artiodactyla, Perissodactyla, Chiroptera, Primates, with probably the Sirenia and Cetacea. We now know that the Hyracoidea also belong to this superorder. In the Archæorhinata were placed the Edentata and Rodentia.

Gymnura has the structures connected with Jacobson's organ almost exactly as in *Erinaceus*, as we should have expected, and very similar to those in *Felis*.

Tupaia and *Macroscelides* have the nasal structures formed, as in the Polyprotodont marsupials, on an entirely different type, and there can be no doubt whatever that they have no near relations with such types as *Erinaceus* and *Gymnura* and must be removed from them and placed in a distinct order, Menotyphla.

In Part II., which will deal with the structures in *Centetes*, *Chrysochloris*, and *Talpa*, will be discussed at greater length the relationships of the different groups.

EXPLANATION OF THE PLATES.

Lettering.

a.r.c., anterior recurrent cartilage; *I.t.*, inferior turbinal; *J.c.*, Jacobson's cartilage; *J.o.* Jacobson's organ; *l.d.*, lacrymal duct; *Mx.*, maxilla; *Na.*, nasal; *n.g.d.*, nasal-gland duct; *n.p.c.*, naso-palatine canal; *n.s.*, nasal septum; *o.b.J.o.*, outer bar of Jacobson's organ; *p.c.*, papillary cartilage; *Pmx.*, premaxilla; *p.n.f.c.*, posterior nasal-floor cartilage; *p.Pmx.*, palatine process of premaxillary; *Vo.*, vomer.

Plate I.

Fig. 1. Section through snout of *Tupaia* sp. across anterior part of premaxilla.
Figs. 2–6. Sections across the snout of *Tupaia* sp., through different regions of the palatine papilla.
Fig. 7. Section through the organ of Jacobson in *Tupaia* sp. a short distance behind the papilla.
Fig. 8. Section through the organ of Jacobson in *Tupaia* sp. towards the posterior part of the organ.

Plate II.

Figs. 9 & 10. Sections across the nose of *Gymnura* a short distance in front of the premaxilla.
Fig. 11. Section across the snout of *Gymnura* in the region of the anterior part of the premaxilla.
Figs. 12 & 13. Sections across the snout of *Gymnura* in the region of the palatine papilla.
Fig. 14. Section across the snout of *Gymnura* immediately behind the papilla.
Fig. 15. Section across the organ of Jacobson in *Gymnura* behind the anterior palatine foramen.
Fig. 16. Section across the posterior part of the organ of Jacobson in *Gymnura*.

All figures are 12 times enlarged.